OCCASIONAL PAPERS
THE MUSEUM
TEXAS TECH UNIVERSITY

NUMBER 135 2 JULY 1990

VARIATION IN THE GLANS PENES AND BACULA AMONG LATIN AMERICAN POPULATIONS OF PEROMYSCUS AZTECUS

ROBERT D. BRADLEY, DAVID J. SCHMIDLY,
AND ROBERT D. OWEN

The Aztec mouse, *Peromyscus aztecus*, is widely distributed throughout the mesic, montane regions of central México, southward to El Salvador and Honduras. *Peromyscus aztecus* is a highly variable species as indicated by the recognition of five subspecies: *P. a. aztecus, P. a. cordillerae, P. a. evides, P. a. hylocetes,* and *P. a. oaxacensis* (Carleton, 1979). Carleton (1979), utilizing morphological variation in the cranium and phallus, hypothesized that these five subspecies represented geographical and elevational variants of the same species; previously, they had been regarded as distinct species (Hooper, 1968). Carleton further hypothesized that *P. aztecus* was closely allied to *P. winkelmanni* and *P. spicilegus*, and that these three species formed a separate phenetic assemblage in the *P. boylii* complex (see Carleton, 1977 and 1979, for further discussion).

Smith *et al.* (1989), using nondifferentially stained chromosomes, examined chromosomal variation among populations of four subspecies of *P. aztecus*. The number of chromosomal arms (FN) in this species ranged from 68 to 74 (Smith *et al.*, 1989), but the pattern of variation was not concordant with the current taxonomic arrangement. Their results indicated that *aztecus*

possessed a karyotype with FN = 68 and 70. The karyotype of *evides* was FN = 68 and appeared identical to the FN = 68 of *aztecus* even though the two taxa are geographically disjunct. Smith *et al.* (1989) also reported the karyotype of *oaxacensis* (FN = 70) to be similar to the FN = 70 form of aztecus. The karyotype of *hylocetes* was variable, with FN ranging from 72 to 74, and possessed the unique sex pair (X and Y chromosomes) as reported by Lee and Elder (1977).

Bradley and Schmidly (1987), in a phenetic and phylogenetic analysis of the glans penes and bacula in the *P. boylii* species complex, studied topotype or near-topotype samples of *aztecus, evides, hylocetes,* and *oaxacensis*. Their analyses revealed a close relationship of *evides* and *hylocetes* to *oaxacensis* and *oaxacensis* to *aztecus*. However, neither their nor Carleton's (1979) study considered geographic variation in phallic characters or compared phenetic variation of the phallus with chromosomal variation. The purpose of this paper is to 1) examine geographic variation in the glans penes and bacula of four subspecies of *P. aztecus* (*aztecus, evides, hylocetes,* and *oaxacensis*) and compare these data with the phenetic and phylogenetic relationships proposed by Bradley and Schmidly (1987); 2) compare the phallic data with the cranial morphology data set of Carleton (1979); 3) compare phenetic variation of the phallus with that of the chromosomal (Smith *et al.*, 1989) and biochemical (C. W. Kilpatrick, personal communication) data sets; and 4) discuss taxonomic implications and correlation of data sets in the *P. aztecus* assemblage.

Materials and Methods

Preparation of the phallus for study followed the method outlined by Bradley and Schmidly (1987) and Bradley *et al.* (1989). Emphasis was placed on using samples with known chromosomal data, as well as including topotypic samples. Where possible, samples were obtained from single localities. In a few cases, however, samples from adjacent or nearby localities were combined to increase sample sizes for statistical analyses (Table 1). These combinations were made only if the samples were chromosomally or morphologically similar, or both. Analysis of variance tests of the Statistical Analysis System (SAS Institute Inc., 1985) were used to determine if nongeographic variation existed among adult age classes (defined according to Schmidly, 1973).

TABLE 1.—*OTU number, sample size, Mexican state, locality, FN (NK = no karyotype), and taxonomic information for samples examined.*

OTU	N	Mexican State	Locality	FN	Taxon
1	20	Michoacán	Mil Cumbres	72-74	*hylocetes*
2	6	Veracruz	Huatusco	68, 70	*aztecus*
3	5	Guererro	Filo de Caballo	NK	*evides*
4	16	Oaxaca	Juquila	68	*evides*
5	10	Oaxaca	Suchixtepec	68	*evides*
6	18	Oaxaca	Llano de las Flores	70	*oaxacensis*
7	17	Chiapas	Pueblo Nuevo	NK	*oaxacensis*
8	8	Chiapas	Yerbabuena	70*	*oaxacensis*

* The sample from Yerbabuena was originally reported to possess an FN = 68 by Schmidly and Schroeter (1974); this was modified to an FN = 70 by Smith *et al.* (1989).

Five qualitative characteristics of each penis were scored from dorsal, ventral, and lateral views as follows: density of spines on the dorsal surface (DSD), density of spines on the ventral surface (DSV), size of spines on the dorsal surface (SSD), size of spines on the ventral surface (SSV), and general shape of the phallus (OP). These characters were coded into 12 presence-absence characters for subsequent analysis (Table 2). Additionally, a single specimen representative of each taxon was examined with the aid of a scanning electron microscope. For this analysis, each phallus was prepared following the methods of Bradley and Schmidly (1987) and Bradley *et al.* (1989), and photomicrographs illustrating various views and structures were taken of each phallus.

Eight quantitative characters of the phallus were measured using an occular micrometer calibrated to the nearest 0.01 millimeter (see Bradley and Schmidly, 1987, and Bradley *et al.* 1989, for definitions and measurements): length of distal tract (LDT), length of glans (LG), length of protractile tip (LPT), greatest width of glans (GWG), length of baculum (LB), length of cartilaginous tip (LCT), width of baculum at base (WBB) and greatest width of baculum at midpoint (GWP). To visualize characters concerning the cartilaginous tip and baculum, a clearing and staining procedure was required (Hamilton, 1946; Hooper, 1958; Lidicker, 1960). These procedures were performed only after a thorough examination of the qualitative and quantitative characters of the glans.

TABLE 2.—*Coding scheme and data matrix for qualitative characters. See text and Bradley and Schmidly (1987) for an explanation of character abbreviations.*

Character State	OTU 1	2	3	4	5	6	7	8
DSD								
dense	0	1	1	0	0	1	1	1
exceptionally dense	1	0	0	1	1	0	0	0
DSV								
dense	0	1	1	0	0	1	1	1
exceptionally dense	1	0	0	1	1	0	0	0
SSD								
quite small	1	0	0	0	0	0	1	1
small	0	1	1	1	0	1	0	0
medium	0	0	0	0	1	0	0	0
SSV								
minute	1	0	0	0	0	0	0	0
quite small	0	1	1	1	0	1	1	1
small	0	0	0	0	1	0	0	0
OP								
rod-shaped	0	1	0	0	0	0	0	0
vase-shaped	1	0	1	1	1	1	1	1

Qualitative and quantitative data sets were used to assess the taxonomic relationships among the eight operational taxonomic units (OTUs). The qualitative characters were used to compute pairwise similarity values using Jaccard's similarity coefficient (Sneath and Sokal, 1973), which disregards matches based on character state absences. The unweighted pair-group method using arithmetic averages (UPGMA) was used to construct a phenogram illustrating phenetic similarities based on the Jaccard coefficients. This phenogram depicted relationships among samples based on traditional nonmetric characteristics of the phallus.

Quantitative characters were standardized to allow for the substantial size differences among character means. The standardized values then were used to calculate average taxonomic distances (Sneath and Sokal, 1973) between samples. A phenogram constructed from these values depicted phenetic relationships among samples based on relative size and shape of the various phallic characters. The (UPGMA) method was used to construct this phenogram as well as the one based on presence-absence characters described previously.

A principal component analysis was conducted using the character correlation matrix of the standardized quantitative characters. This analysis allowed us to determine which characters are important in differentiating morphometrically among samples. Projection of the sample mean scores onto the first three components in a three-dimensional diagram allowed us to assess visually the clusters among samples. A minimum spanning tree superimposed onto this diagram helped determine the shortest path among samples and to infer whether relationships were accurately represented by the three-dimensional diagram. All analyses were conducted using the Numerical Taxonomy System of multivariate statistical programs (Rohlf *et al.*, 1979).

Results

Description of Phalli

The glans penis of *P. aztecus* is vase-shaped and medium in size (length about four times the width) for the *P. boylii* species complex (Fig. 1). The surface of the glans is covered with recurved spines that are longer than wide, with spines on the dorsum slightly larger than those on the ventral surface. Spines near the protractile tip are slightly smaller and denser than those near the base of the glans. Furrowing is well pronounced and dorsal and ventral lappets are absent. The baculum is rod-shaped, slightly curved laterally, approximately 1.3 to 1.4 times longer than the glans penis, and possesses a minute cartilaginous tip. See Bradley and Schmidly (1987) for a more detailed description of the phallus for each subspecies, as well as comparison with other phallic types in the *P. boylii* complex.

The primary quantitative differences among the four subspecies of *P. aztecus* reflect gradations in overall size of the phallus, with *evides* having the largest structure, followed by *oaxacensis, hylocetes*, and *aztecus*. Qualitative differences are reflected by the denser distribution of dorsal and ventral spines in *hylocetes* and two samples of *evides* (OTUs 4 and 5), and the rod-shaped glans of *aztecus* compared to the vase-shaped glans of *evides, hylocetes*, and *oaxacensis*.

Nongeographic Variation

Analysis of variance revealed no significant differences in measurements of quantitative characters among the three adult

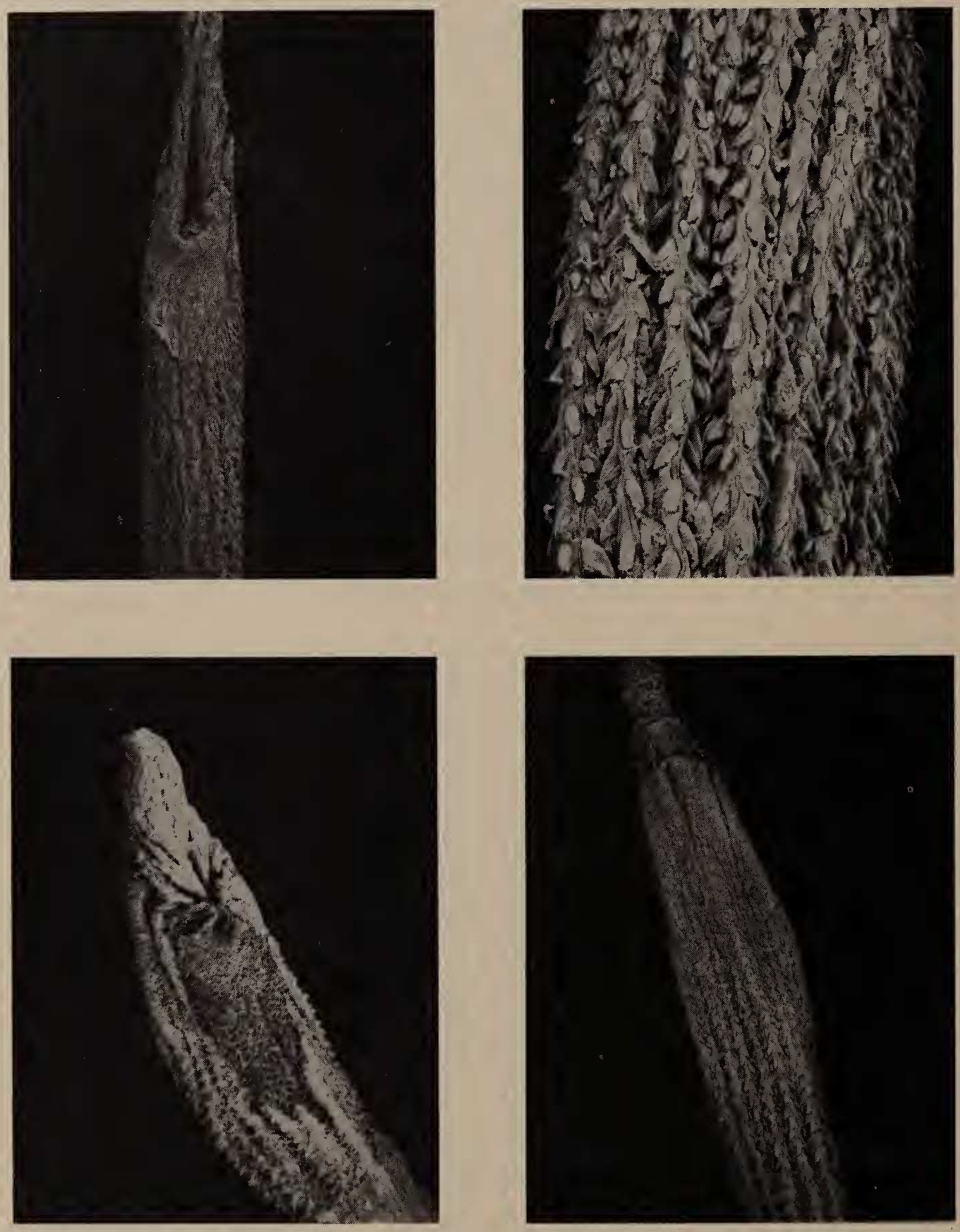

FIG. 1.—Scanning electron photomicrographs showing epidermal structures and distribution of spines on the glans penes of *P. a. aztecus* (top left), *P. a. evides* (top right), *P. a. hylocetes* (bottom left), and *P. a. oaxacensis* (bottom right).

age classes ($P < 0.001$ in all cases) for the four samples with the largest sample sizes (OTUs 1, 4, 6, and 7). Based on these results, adult age classes IV, V, and VI were combined for subsequent analyses. Additionally, the polymorphic karyotypes in OTU 1 and OTU 2 were combined, respectively, because no

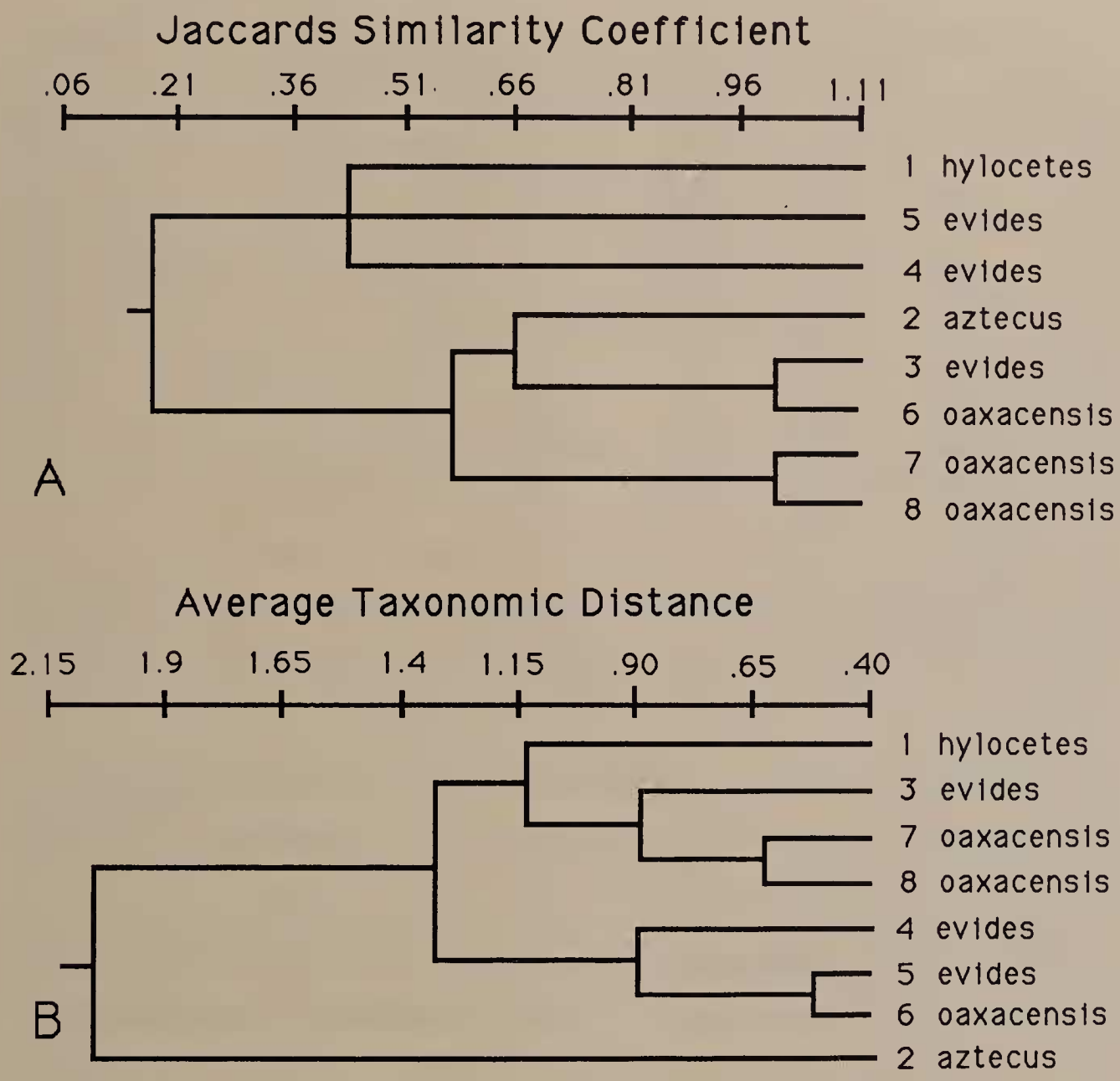

FIG. 2.—Phenograms depicting relationships of the eight OTUs based on A) qualitative characters using Jaccard's Similarity Coefficient, and B) quantitative characters using average taxonomic distance. Both phenograms were constructed by the unweigted pair-group method using arithmetic averages (UPGMA). Cophenetic correlation coefficients were 0.92 for both phenograms.

detectable qualitative or quantitative differences existed among phalli of the polymorphic chromosomal groups in this study, and because Bradley *et al.* (1989) reported no variation in a similar study among polymorphic chromosomal groups of *P. beatae* and *P. l. ambiguus*.

Geographic Variation

The phenogram (Fig. 2A) based on Jaccard's similarity coefficients of presence-absence (qualitative) characters had a cophenetic correlation coefficient of 0.92, indicating relatively little distortion in representation of the similarity matrix. The phenogram depicts two primary clusters, although some members

TABLE 3.—*Character means for OTUs examined in this study. See text and Bradley and Schmidly (1987) for explanation of character abbreviations.*

OTU	LDT	LG	LPT	GWG	LB	LCT	WBB	GWP
1	10.93	7.04	2.03	1.75	9.71	0.16	1.20	0.29
2	10.48	6.22	1.98	1.62	8.77	0.13	0.96	0.38
3	10.46	7.35	1.93	1.87	9.38	0.17	1.25	0.33
4	11.93	7.53	2.26	1.94	9.72	0.15	1.24	0.32
5	11.68	7.36	2.21	1.86	10.28	0.17	1.30	0.36
6	11.25	7.36	2.16	1.86	10.07	0.17	1.32	0.33
7	10.49	6.52	1.96	1.84	9.37	0.17	1.33	0.35
8	10.47	6.43	2.12	1.83	9.26	0.18	1.23	0.36

of each group are related by low identity levels (< 0.5). The first cluster consists of OTUs 1 (*hylocetes*) and 4 and 5 (*evides*), which are related at a level of 0.43. The second cluster contains all three samples of *oaxacensis* (OTUs 6, 7, and 8), and shows OTUs 3 (*evides*) and 6 (*oaxacensis*) to be identical based upon the qualitative characters. The second cluster also includes the *aztecus* sample (OTU 2), although it forms a separate subcluster at a similarity level of 0.67.

The phenogram (Fig. 2B) based on average taxonomic distances computed from the quantitative characters has a cophenetic correlation coefficient of 0.92, and includes three relatively well-delineated clusters. Populational means for each quantitative character are given in Table 3. OTU 2 (*aztecus*) is the most distinct group defined in the analysis. Of the remaining taxa, OTUs 4 and 5 (*evides*) and 6 (*oaxacensis*) form a cluster as do OTUs 3 (*evides*), and 7 and 8 (*oaxacensis*). OTU 1 (*hylocetes*) is loosely allied with the latter cluster.

Results of the principal component analysis are shown in Figure 3. The first three components account for 57.8, 20.5, and 12.3 percent of the variation, respectively. Component I, generally representing a size factor, has high positive loadings for all characters except GWP (Table 4). Component II is positively correlated with LCT, and (to a lesser degree) with WBB, and is negatively correlated with LDT and LPT. Component III reflects a high negative correlation with GWP. The minimum-spanning tree superimposed on the principal component projections indicates that relatively little distortion of relationship among samples occurs in reduction to three axes. This tree describes the same three clusters that were found in the quantitative-character phenogram (Fig. 2B). Specimens

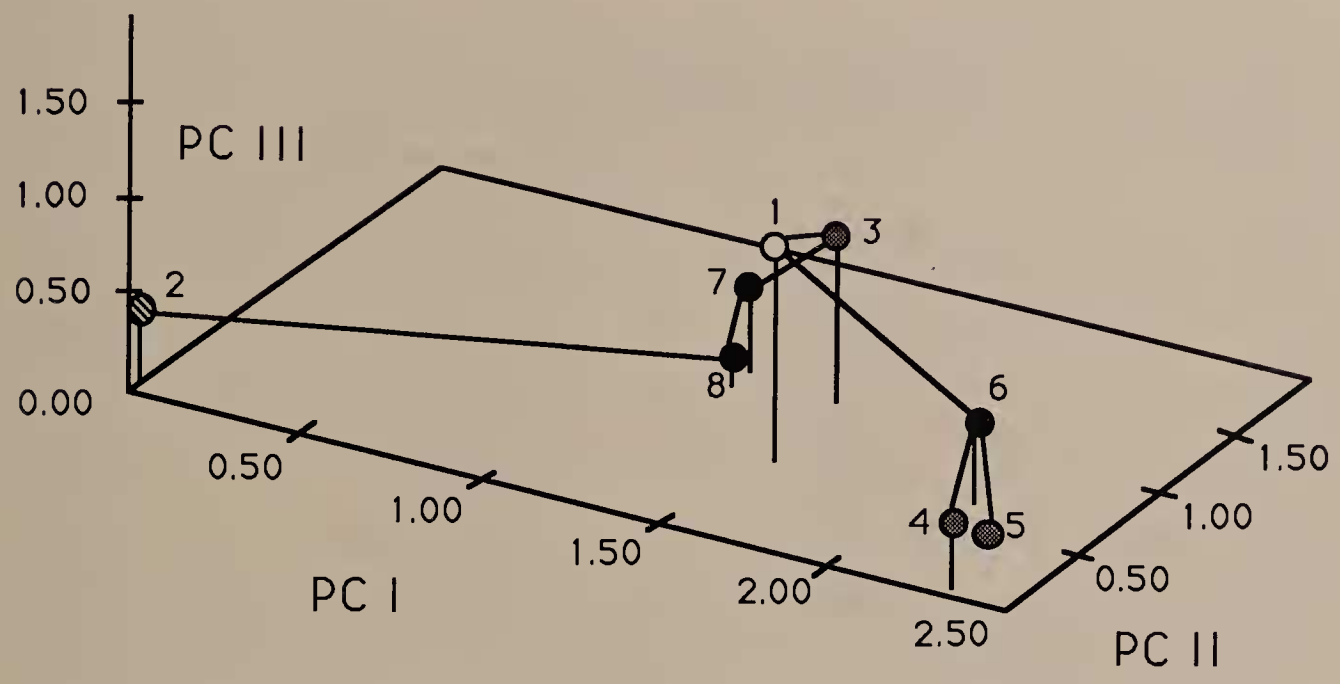

FIG. 3.—Principal component projection of quantitative characters with the minimum spanning tree analysis superimposed. The first three components account for 57.8, 20.5, and 12.3 percent of the total variance, respectively.

from OTU 2 (*aztecus*) have small phalli, whereas OTUs 4, 5, and 6 have the largest phalli. OTUs 3, 7, and 8 have larger values for Component II characteristics, reflecting large LCT and WBB values or smaller values for LPT and LDT, or both. OTU 1 (*hylocetes*) is characterized by a high Component III value reflecting small values for GWP.

DISCUSSION

Comparisons of the quantitative data from the average taxonomic distance, principal component, and minimum-spanning tree analyses (Fig. 2B and 3) depict three clusters, which show nearly identical relationships among the samples examined. The first cluster contains only the *aztecus* sample (OTU 2), which is among the smallest in size for all characters examined except GWP for which it has the largest values, and is reflected along Component I. The second cluster is comprised of two samples of *evides* (OTUs 4 and 5) and one sample of *oaxacensis* (OTU 6). These three samples are characterized by a large glans and baculum along Component I and medium to small values for LCT and WBB and large values for LPT and LDT along Component II. The third cluster contains two samples of *oaxacensis* (OTUs 7 and 8), one sample of *evides* (OTU 3), and the sample of *hylocetes* (OTU 1). These samples are characterized by a combination of small values for LDT and LPT, and large values for LCT and WBB (the reverse of the second cluster).

TABLE 4.—*Character loadings for the first three principal components for eight samples of* P. aztecus, *using quantitative characters.*

Character	Principal Component		
	I	II	III
LDT	0.722	-0.618	-0.097
LG	0.869	-0.191	0.290
LPT	0.700	-0.505	-0.401
GWG	0.867	0.235	-0.109
LB	0.912	-0.078	-0.041
LCT	0.529	0.786	-0.203
WBB	0.812	0.533	-0.092
GWP	-0.511	-0.030	-0.817

Comparison of the qualitative (Fig. 2A) and quantitative (Fig. 2B and 3) results, however, show several incongruencies between the two data sets. The quantitative data depict *aztecus* (OTU 2) as distinct from other samples based on its small size. The qualitative data, however, show it to be similar to the three samples of *oaxacensis* (OTUs 6, 7, and 8) and one sample of *evides* (OTU 3). Although the qualitative and quantitative analyses show a close relationship of two of the three samples of *oaxacensis* (OTUs 7 and 8), placement of the third sample (OTU 6) is inconsistent. The qualitative data show OTU 6 (*oaxacensis*) more closely resembles OTU 3 (*evides*) and OTU 2 (*aztecus*) than to the other two samples of *oaxacensis*, whereas the quantitative data show a close affinity of OTU 6 to *evides* (OTUs 4 and 5) and a more distant relationship to the other two samples of *oaxacensis*. The three samples of *evides* (OTUs 3, 4, and 5) show a similar pattern of inconsistences, with OTUs 4 and 5 being similar, but with OTU 3 being allied to various samples of *oaxacensis*. The sample of *hylocetes* (OTU 1) consistently is related to *evides*, albeit to OTUs 4 and 5 in the qualitative analysis and to OTU 3 in the quantitative analyses.

The qualitative data presented herein corroborate the phylogenetic relationships proposed by Bradley and Schmidly (1987) for the *aztecus* assemblage with the exception of the *evides* sample (OTU 3), which here is placed in the *oaxacensis-aztecus* cluster. Using qualitative characters from topotype samples, Bradley and Schmidly (1987) reported that *aztecus* and *oaxacensis* formed a single clade and *evides* formed a sister group to the *hylocetes* and *P. spicilegus* clade. The placement of the *evides* sample (OTU 3) may not be as misleading as it seems, for this sample is from Filo

de Caballo, Guerrero, and lies at the extreme northwestern edge of the range of *evides*. The geographic distance separating the Guerrero and Oaxaca samples may account for the morphological variation existing in *evides*.

One of the major conclusions of Carleton's (1979) study of the taxonomic relationships of *P. aztecus* was that subspecific variation was reflected by the size of morphological characters, with *hylocetes* being the largest in size, followed by *oaxacensis, evides,* and *aztecus*. Our phallic data do not reflect this pattern of size gradation as *evides* is the largest in size, followed by *hylocetes, oaxacensis*, and *aztecus*. Carleton (1979) also suggested that the increase in size of cranial characters was correlated with an increase in elevation. An examination of the elevational values from our study regressed against the first principal component score revealed a nonsignificant correlation between elevation and subspecific divergence ($r^2 = 0.00$, $P > 0.976$). However, it should be emphasized that Carleton's data were comprised of cranial characters, which may not be congruent with the phallic data set.

Smith *et al.* (1989) presented chromosomal data for *aztecus* and *evides* and summarized the existing variation within *P. aztecus*. Their data showed *evides* (FN = 68) and *oaxacensis* (FN = 70) to have karyotypes similar to that of *aztecus* (FN = 68, 70). Only *hylocetes* (FN = 72-74) possessed an unique karyotype. Without chromosomal banding data, it is impossible to distinguish between the karyotypes of *aztecus, evides*, and *oaxacensis*. However, no apparent correlation exists between the pattern of karyotypic variation and that found in the phallus. It should be noted no karyotypic data were available for the sample of *evides* (OTU 3), which consistently failed to cluster with other samples of *evides* (OTUs 4 and 5). In a biochemical analysis, this same sample grouped closer to *P. winkelmanni* than to any other *P. aztecus* sample (C. W. Kilpatrick, personal communication). These data suggest that the sample of *evides* from Guerrero may be distinct from samples from Oaxaca.

The qualitative data and the phylogenetic study of Bradley and Schmidly (1987) compared with the known geographic distribution of the four subspecies of *P. aztecus* may provide a plausible explanation for the divergence of this group. The four subspecies occupy different mountain ranges in central and southern México, with *aztecus* inhabiting the Sierra Madre Oriental in Puebla and

Veracruz, *oaxacensis* the highlands in Oaxaca and Chiapas where the Sierra Madre Oriental and Sierra Madre del Sur meet, *evides* the Sierra Madre del Sur region of Oaxaca and Guerrero, and *hylocetes* the Cordillera Transvolcanica zone of Jalisco. If one assumes a southern origin for this species (see Carleton, 1977 and 1979, for further discussion) and an *oaxacensis*-like ancestor (the most wide-ranging taxon), then dispersal northward along the Sierra Madre Oriental could have given rise to the *aztecus* type, and dispersal to the west along the Sierra Madre del Sur and Cordillera Transvolcanica ranges could have produced *evides* and *hylocetes*. Alternatively, if one assumes that *P. aztecus* forms the ancestral stock for the remaining three subspecies, then the *aztecus-oaxacensis-evides-hylocetes* relationship would result from a clockwise radiation into these mountain ranges of central and southern México. Obviously, a cladistic analysis of G-band chromosomes is needed to determine which taxon possesses the primitive karyotype necessary for testing the origin of these subspecies.

As a result of a lack of congruence among data sets, it is difficult to resolve the taxonomic relationships of the four subspecies of *P. aztecus*. First, the qualitative and quantitative data are incompatible, although the qualitative data herein support the phylogenetic study of Bradley and Schmidly (1987). The qualitative data (this study; Bradley and Schmidly, 1987) show a close relationship of *aztecus* to *oaxacensis* and *evides* to *hylocetes*. The quantitative data, on the other hand, depict *aztecus* as being distinct from the other three subspecies. The incongruence of the qualitative and quantitative data sets herein is suggestive of that found in a similar study of phallic characters in *P. boylli, P. beatae*, and *P. levipes* (Bradley *et al.*, 1989). Second, neither data set is congruent with Carleton's (1979) hypothesis of elevation zones being correlated with morphological variation. Third, the phallic data set is not concordant with the chromosomal variation reported by Smith *et al.* (1989). The difficulty in resolving the taxonomy of *P. aztecus* is similar to the situation that has existed in *P. boylii, P. beatae*, and *P. levipes* (Houseal *et al.*, 1987; Rennert and Kilpatrick, 1986, 1987; Schmidly *et al.*, 1988; Bradley and Schmidly, 1987; Bradley *et al.*, 1989). Complete and independent data sets will be needed for further taxonomic resolution of this group.

Acknowledgments

We thank T. W. Houseal, S. A. Smith, K. M. Davis, J. Ensink, M. W. Allard, D. Werbitsky, P. D. Rennert, C. W. Kilpatrick, I. F. Greenbaum, and D. W. Hale for their assistance in obtaining specimens. We also are indebted to A. C. Carmichael, The Museum, Michigan State University, and P. Myers and L. R. Heaney, University of Michigan Museum of Zoology, for allowing us to borrow specimens. Special thanks to H. Sittertz-Bhatkar for preparing the scanning electron microscope photomicrographs, and to the Texas Agriculture Experiment Station for supporting that aspect of the research. We also thank J. N. Derr, K. L. Bowers, and L. C. Bradley for comments and assistance during various stages of this manuscript.

The research was supported by the National Science Foundation through grants DEB 81-17447 (I. F. Greenbaum and D. J. Schmidly) and DEB 81-18966 (C. W. Kilpatrick). We thank the Dirección General de Flora y Fauna Silvestres for granting permission to collect in México, and the numerous faculty and students at Universidad Nacional Autónoma de México who aided our work in México. This paper represents contribution number TA-25156 of the Texas Agricultural Experiment Station.

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Addresses of authors: *Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, Texas 77843 (RDB, DJS); The Museum, Texas Tech University, Lubbock, Texas 79409 (RDO).* Present addresses: *Department of Biological Sciences, Texas Tech University, Lubbock, Texas 79409 (RDB); Department of Biology, University of Missouri-Kansas City, Kansas City, Missouri 64110 (RDO) .* *Received 4 December 1989; accepted 13 December 1989.*

APPENDIX.—*List of specimens examined.—Sample numbers and karyotypic data are as shown in Table 1. All localities are in México unless otherwise indicated. Museum designations are as follows: MSU, The Museum, Michigan State University; TCWC, Texas Cooperative Wildlife Collections, Texas A&M University; UMMZ, Museum of Zoology, University of Michigan.*

Peromyscus aztecus aztecus.—OTU 2. HIDALGO: 13.0 mi. NE Metepec, 6600 ft., 3 (UMMZ). PUEBLA: 1.0 mi. SW Huachinango, 1 (TCWC). VERACRUZ: 1.4 mi. SSW Huatusco, 1 (TCWC); 5.5 mi. N Huatusco, 1 (TCWC).

Peromyscus aztecus evides.—OTU 3. GUERRERO: Filo de Caballo, 7900 ft., 1 (TCWC); Omilteme, 1 (UMMZ); Puerto Chico (63 km. SW Casa Verde) 8400 ft., 1 (UMMZ); 12.0 mi. SW Xochipala, 8200 ft., 2 (MSU). *OTU 4.* OAXACA: Juquila (Santa Rose), 1300 m., 2 (UMMZ); 4.0 mi. E Juquila, 6000 ft., 1 (TCWC); 5.0 mi. E Juquila, 6000 ft., 1 (TCWC); 6.0 mi. E Juquila, 6000 ft., 12 (TCWC). *OTU 5.* OAXACA: 3.0 mi. S Suchixtepec, 7100 ft., 8 (TCWC); 4.0 mi. S Jalatengo, 5000 ft., 1 (UMMZ); Campemento Río Molino, 7300 ft., 1 (UMMZ).

Peromyscus aztecus hylocetes.—OTU 1. MICHOACAN: 2.2 mi. W Mil Cumbres, 3 (TCWC); 2.3 mi. W Mil Cumbres, 1 (TCWC); 2.5 mi. W Mil Cumbres, 1 (TCWC); 3.9 mi. W Mil Cumbres, 2 (TCWC); 5.3 mi. W Mil Cumbres, 1 (TCWC); 12.0 mi. W Mil Cumbres, 2 (TCWC); 1.6 mi. S Los Azufres, 2 (TCWC); 3.0 mi. S Los Azufres, 1 (TCWC); 5.7 mi. S Los Azufres, 1 (TCWC); 2.0 mi. E Opopeo, 2 (TCWC), 0.3 mi. W Puerta Garnica (Parque National), 2 (TCWC). MORELOS, 1.5 mi. W Huitzilac, 2 (TCWC).

Peromyscus aztecus oaxacensis.—OTU 6. OAXACA: 0.9 mi. N Llano de Las Flores, 9200 ft., 5 (TCWC); 12.0 mi. N Ixtlan de Juarez (Llano de Las Flores), 9200 ft., 11 (UMMZ); 13.0 mi. N Llano del Las Flores (Cerro Pelón), 2,700 m., 2 (UMMZ). *OTU 7.* CHIAPAS: 1.0 mi. N Pueblo, 5500 ft., 14 (UMMZ); 8.0 mi. SE San Christobal de la Casas, 7800 ft., 3 (UMMZ). *OTU 8.* CHIAPAS: Yerbabuena, 5 (UMMZ). GUATEMALA: Sololá, Soloá, 1 (UMMZ); Escuintla, Escuintla, 1 (UMMZ); Huehuetenango, La Libertad, 1 (UMMZ).